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Monitoring pelagic ecosystems using plankton indicators

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Planktonic organisms are an important food resource of pelagic ecosystems, but they also serve as an integrator of hydroclimatic forcing. Four types of recently developed plankton indicator, based on the Continuous Plankton Recorder survey, are summarized here: indicators based on individual taxa; indicators based on functional attributes of the ecosystem (diversity); species assemblage indicators; and indicators of larval fish survival. All provide information on the state of a pelagic ecosystem, but have different limitations. Therefore, their combined application provides the most accurate diagnosis of ecosystem state. In most of the examples described, statistical analyses help to identify major spatial and temporal patterns, and may allow future ecosystem changes to be anticipated.

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Introduction

With a multitude of direct or indirect anthropogenic influences, in addition to the confounding effects of natural variability of the marine environment (Hare and Mantua, 2000; Reid and Planque, 2000), management of marine ecosystems to achieve sustainable exploitation represents a real challenge.

Plankton plays an important role in the functioning of marine ecosystems and in biogeochemical cycles (Roemmich and McGowan, 1995), because it is a key component of the trophodynamics of pelagic ecosystems. Because planktonic organisms represent a major source of energy for fish, at least at some stage of their life cycle (Cushing, 1997), there is a direct link with fish even if this link may only exist during a short period of time (e.g. *Calanus finmarchicus* and larval cod; Thorisson, 1989; Munk, 1997). Plankton also represents the first level of integration of hydroclimatic forcing in the pelagic foodweb.

Many studies using the Continuous Plankton Recorder (CPR) data set have documented relationships between plankton and hydrometeorological changes in the North Atlantic Ocean (Colebrook, 1991; Fromentin and Planque, 1996; Beaugrand and Reid, 2003), and many suggest that plankton may be used as an indicator of climate change (Reid and Edwards, 2001). In particular, temperature is a key parameter affecting physiological rates at the individual level (e.g. enzymatic reactions, respiration, rates of feeding), impacting growth rate, body size, and generation time (Peters, 1983; Mauchline, 1998). Wind has an effect on water turbulence, which in turn influences the behaviour of individuals, encounter rates between prey and predator (Mackenzie and Legget, 1991), and metabolism (Alcaraz, 1997; Margalef, 1997). These microscale effects of hydroclimatic forcing on plankton occur permanently, each species integrating the effects over its generation time, and transferring the integrated effect to the next generation. Therefore, effects of hydroclimatic variability on individual organisms may ultimately have a strong impact on the whole ecosystem. Because the temperatures experienced by marine life may differ from temperatures measured by sensors (Ottersen *et al.*, 1994), it is not surprising that the link between plankton and larval fish can be tighter than the link between temperature and larval fish (Beaugrand *et al.*, 2003).

This paper focuses on plankton indicators that can be derived from the CPR survey. Among the many possible plankton indicators that can be derived from this data set, four recently developed types that may be used to monitor the dynamic regime (or state equilibrium; Scheffer *et al.*, 2001) are summarized here, based on: (i) abundance of individual taxa; (ii) functional attributes of the ecosystem; (iii) species assemblages; and (iv) larval fish survival.
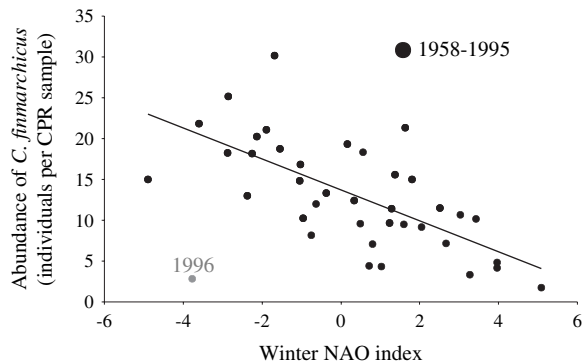
Figure 1. Relationship between mean CPR abundance of *Calanus finmarchicus* in the North Sea and the winter North Atlantic Oscillation index, 1958–1996.

Abundance of individual taxa

Commonly used plankton indicators are often based on individual taxa. Figure 1 shows the relationship between the abundance of *Calanus finmarchicus* and the state of the
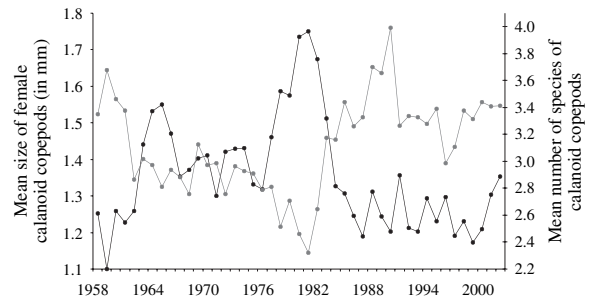

Figure 2. Long-term changes in calanoid copepods in the North Sea: mean size of females (black) and mean number of species per CPR sample (grey; after Beaugrand, 2003).

North Atlantic Oscillation (NAO). After finding this relationship, Fromentin and Planque (1996) hypothesized that the link occurred via surface climate forcing on production of *C. finmarchicus*, and through interspecific competition with its congener *C. helgolandicus*. The strong relationship encouraged Planque and Reid (1998) to forecast the abundance of *C. finmarchicus* from the winter
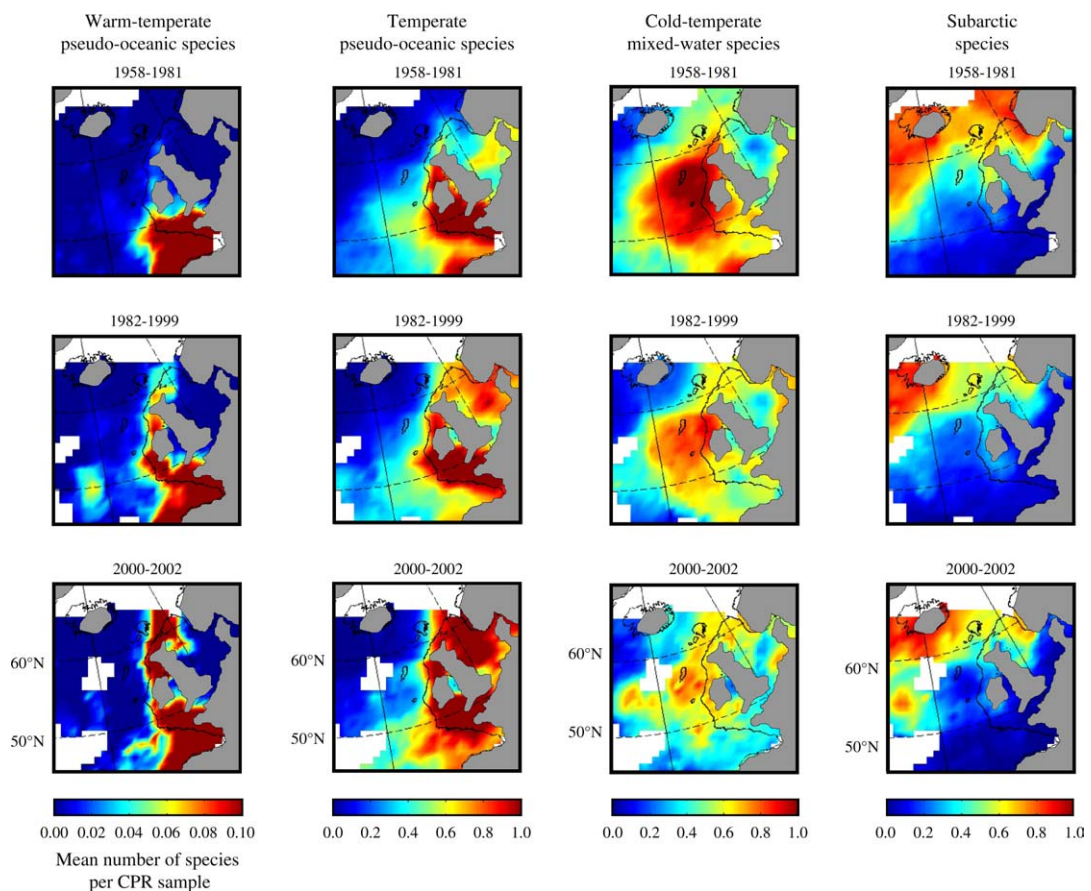

Figure 3. Long-term changes in the mean number of species per assemblage based on three periods: 1958–1981, 1982–1999, and 2000–2002 (recalculated after Beaugrand *et al.*, 2002c).

NAO index. However, the relationship apparently broke down after 1995 (Figure 1). To explain this disruption, Heath *et al.* (1999) suggested that abundance depends on two factors: the volume of over-wintering habitat (Norwegian Sea Deep Water), and spring advection from this habitat to the North Sea. Although their study allowed a better understanding of hydroclimatic parameters affecting the North Sea ecosystem, it also indicated that use of a single-species plankton indicator is limited, even if it is a key species in the region, because it does not allow inferences about the entire plankton ecosystem to be drawn (Beaugrand and Reid, 2003). Although such indicators may be occasionally useful, monitoring changes in ecosystems by means of single taxa may be quite arbitrary, because variable features related to factors such as aggregation or dispersal, as well as mortality or survival, may influence the distribution of pelagic organisms (Colebrook *et al.*, 1961).

Functional attributes of the ecosystem

Recently, indicators of long-term variations in ecosystem state have been developed that are based on a large amount of information. Examples are the diversity and mean size of calanoid copepods in the North Sea (Figure 2; Beaugrand, 2003; Beaugrand *et al.*, 2003). Diversity increased sharply in the early 1980s, coinciding with a decline in the mean size of female calanoid copepods. Reid *et al.* (2001) suggest a regime shift in North Sea ecosystems around 1988. Although the two indicators do not support a marked regime shift at about that particular year, they do show stepwise changes after the beginning of the 1980s as well as the impact of a cold biological episodic event (1978−1982), as described recently by Edwards *et al.* (2002). This suggests that the regime shift in the North Sea has modified ecosystem structure, which may have powerful consequences for exploited resources and biogeochemical cycles in the region. Using synthetic indicators such as diversity indices may be useful in detecting a change, but interpretation is difficult, because they do not provide clues to understand the changes.

Species assemblages

To further understand the changes in calanoid copepod (one of the taxonomic groups sampled best by the CPR survey) diversity that took place in the North Sea, Beaugrand *et al.* (2002a) recently decomposed this group into species assemblages, using geostatistics and multivariate analyses in combination with the "Indicator Values" method designed by Dufrêne and Legendre (1997). At the scale of the North Atlantic basin, and with a spatial resolution approaching the mesoscale (about 200 km), nine species assemblages were identified using three criteria: (i) spatial distribution, (ii) similarity in seasonal variability, and (iii) similarity in diel and ontogenetic variations. The nine
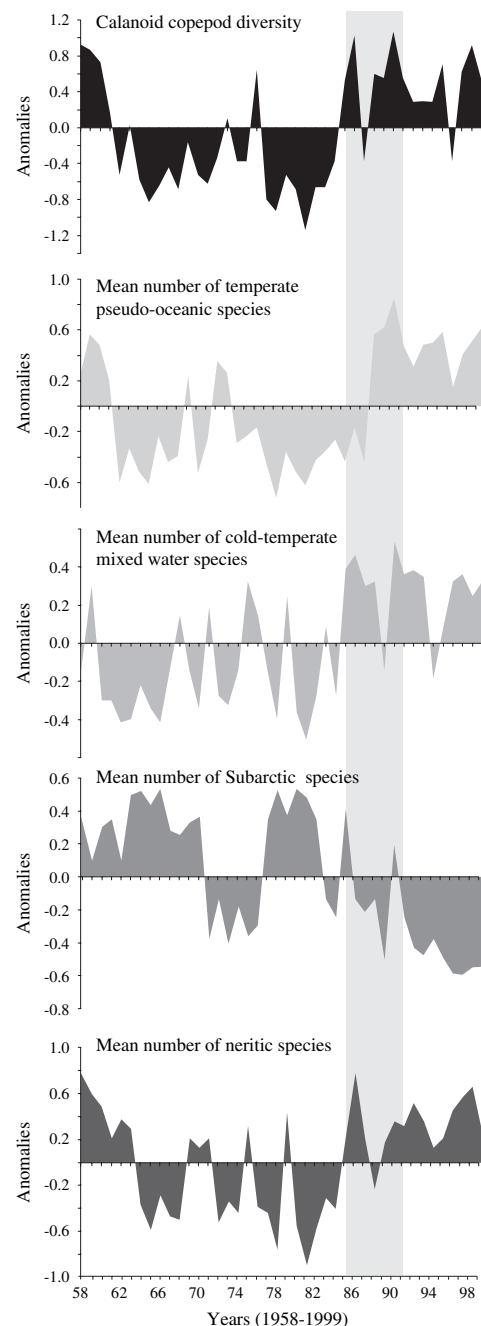

Figure 4. Long-term changes in total calanoid copepod diversity (mean number of species) and in the diversity of different species assemblages in the North Sea region (based on Beaugrand, 2004a).

assemblages (for details, see Table 1 in Beaugrand *et al.*, 2002a) were closely related to a stable-biotope (e.g. geographical location linked bathymetry) or substrate-biotope component (e.g. current), *sensu* van der Spoel (1994). The mean number of species per assemblage was used as an

indicator of change in the biogeographical range of copepod communities, and of modifications in ecosystem functioning (for details see Beaugrand, 2004a). Beaugrand *et al.* (2002b) document major biogeographical shifts for all assemblages since the early 1980s in the area southwest of the British Isles, and from the mid-1980s in the North Sea. Values for four species assemblages around the United Kingdom were recalculated for three periods (1958−1981, 1982−1999, and 2000−2002; Figure 3). The number of warm-temperate and temperate pseudo-oceanic assemblages increased northwards, while the number of cold mixed water and Subarctic assemblages decreased. All assemblages showed consistent long-term changes that appear to reflect a movement of marine ecosystems towards a warmer dynamic regime.

Figure 4 shows the long-term changes in the species assemblages that contributed to the change in overall diversity of calanoid copepods in the North Sea. The observed North Sea regime shift may be part of a larger scale feature (Figure 3), which may have started at the beginning of the 1980s in the southeastern part of the North Atlantic Drift Province (Longhurst, 1998), and progressively spread northwards to 60°N in the mid-1980s. Causes of these changes are complex and may represent the consequence of large-scale hydroclimatic forcing on both the substrate-biotope and stable-biotope component of the pelagic ecosystem.

Larval fish survival

Beaugrand *et al.* (2003) propose a plankton index that integrates biological parameters important for larval cod survival, incorporating information on calanoid copepod biomass, mean size of calanoid copepod prey, and on the abundance of three key prey species (*C. finmarchicus*, *C. helgolandicus*, and *Pseudocalanus* spp.). This index reveals a clear distinction between the period 1963−1983 and both 1958−1962 and 1984−1999 (Figure 5). The period 1963−1983 (encompassing the so-called "gadoid outburst") was characterized by great abundance of prey for larval cod (positive anomalies in calanoid copepod biomass and in the abundance of the three key prey species), and a large mean prey size. Cod recruitment decreased from the mid-1980s, coincident with unfavourable changes in the plankton ecosystem, compared with earlier years. The results provide evidence that changes in the plankton ecosystem may be the cause of temporal variations in cod recruitment.

Discussion and conclusions

This summary emphasizes the diversity of indicators that can be derived from the CPR survey. Indicators based on abundance of individual taxa are simple, and they have a straightforward interpretation in the case of abundant species. However, for uncommon species, the interpretation may become more complex, more biased by factors such as expatriation from the pelagic realm, misidentification, and contamination from one sample to another. If such species are used, robust statistical analysis should be utilized to filter the information and quantify the confidence limits on the observed changes.

Indicators based on functional attributes are sensitive and may detect subtle changes in a pelagic ecosystem. For example, the regime shift in the North Sea (Reid *et al.*, 2001), also evident using the greenness index (Reid *et al.*, 1998; Beaugrand, 2004b), is detected at the beginning of
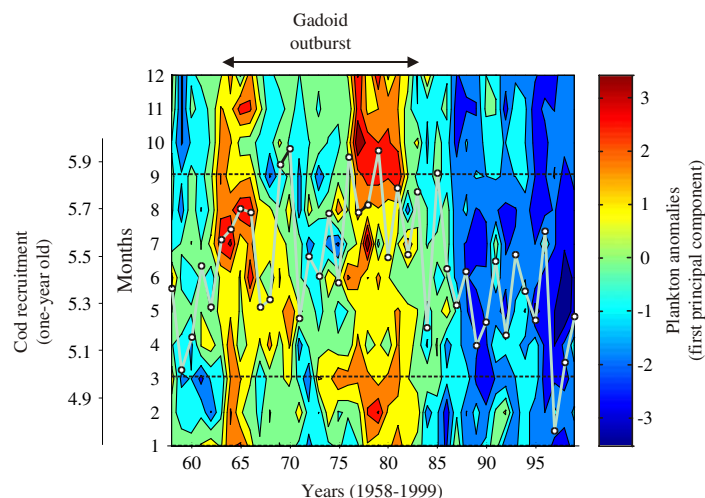

Figure 5. Long-term monthly changes (1958−1999) in the plankton index of larval cod survival (modified from Beaugrand *et al.*, 2003) and recruitment at age one (1-year lag; white). Recruitment data are in decimal logarithm. These data were derived from virtual population analysis (Shepherd, 1996).

the 1980s using an index of species diversity and the mean size of calanoid copepods. The change seen in mean size after the shift (Figure 4) must indicate a change in community structure, and possibly the dynamic regime of the North Sea. The drawback of indicators based on ecosystem functional attributes lies in the fact that they try to capture ecosystem state in a single value. The index mean number of calanoid copepod species per CPR sample has allowed the detection of episodic oceanographic events in the North Sea, as well as a decreasing trend in diversity in oceanic areas. However, the index does not provide enough information to understand the nature of the observed changes. The use of species assemblage indicators brought additional missing pieces to the jigsaw puzzle, leading to the hypothesis that climate change may represent a strong driver in the recent reorganization of North Atlantic ecosystems. The concept of species assemblage indicators might be more widely used. They are rich in information and are sensitive. Moreover, they may lead to a better understanding of the resilience (as defined by Holling, 1973) of pelagic ecosystems and therefore allow future changes to be anticipated.

Acknowledgements

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